# CEANOTHUS OPHIOCHILUS (RHAMNACEAE): A DISTINCTIVE, NARROWLY ENDEMIC SPECIES FROM RIVERSIDE COUNTY, CALIFORNIA

Steve Boyd, Timothy Ross, & Laurel Arnseth

Rancho Santa Ana Botanic Garden, Claremont, California 91711, U.S.A.

### ABSTRACT

A newly discovered species, Ceanothus ophiochilus, is described from Riverside County, California. Unusually small, narrow, semi-terete leaves distinguish this species from other members of section Cerastes. Its blue to pinkish lavender flowers, rather than white, further separate the taxon from other members of the section in southern California. The solitary population is restricted to an unusual pyroxenite rich outcrop on privately held land being considered for development.

KEY WORDS: Ceanothus, Cerastes, Rhamnaceae, edaphic endemic, pyroxenite endemic, endangered species.

#### INTRODUCTION

The species of Ceanothus section Cerastes are characterized by persistent, coriaceous leaves with stomata in sunken pits; thick, darkly colored, corky stipules; and flowers in axillary umbels. All but two species have opposite leaves and most have capsules bearing three horns (McMinn 1942; Munz 1974). Raven (1977) reports that of the 21 species in the section, 20 occur in California, with 17 endemic to the California Floristic Province. The section is especially well represented in the central and northern part of the state, where several of the taxa are edaphic endemics. At least two species are confined to serpentine soils (Nobs 1963; Kruckeberg 1984); one is limited to Franciscan marine sandstones of Jurassic age; and five are restricted to Pliocene Sonoma volcanics (Nobs 1963). Depending on which treatment is followed, seven to eight taxa, representing five or six species and four varieties, have traditionally been recognized for Southern California (McMinn 1942; Munz 1959, 1974). In this paper, we describe a narrowly endemic species of Ceanothus, section

Cerastes, which we encountered in March, 1989, while conducting floristic surveys of a large, privately held parcel surrounding Vail Lake in southwestern Riverside County, California. This plant is an edaphic endemic and is known only from the type locality where it is restricted to an unusual, pyroxenite rich outcrop. The continued existence in the wild of this attractive species is threatened by potential urbanization of the site.

### TAXONOMY

Ceanothus ophiochilus Boyd, Ross, & Arnseth, sp. nov. Figure 1

Frutex rotundatus, ramosissimus, (3.0-) 12-15 (-20.) dm altus. Caules basilares 1-aliquot, trunco principale ad 7.2 cm diametro basi, interdum aspectu funis textilem. Cortex laevis comparate, cinereus ad schistaceum vel castaneum in veteribus truncis decorticantibus. Rami divaricati, cinerei, internodiis (2.0-) 2.5-7.0 (-13) mm longis; ramis hornotinis ferrugineis, pilos parcos breves gerentibus, mox glabrescentibus; stipulis hornotinis ferrugineis, sed maturis ferro-griseis, suberosis. Folia opposita, glabra, coriacea, fasciculata in ramis maturis, flavovirentia ad viridia, ambitu angusteoblanceolata ad obovata, (2.0-) 3.5-7.0 mm longa, (1.0-) 1.5-2.5 (-3.0) mm lata, supra concava subtus gibbosa, 0.8-1.0 mm crassa; apicibus denticulatibus vel rotundatibus vel emarginatibus; marginibus integris vel 1-2 (-3) paribus denticulatibus; costis distinguibilibus sed nervatura secundaria obscura generaliter; petiolis 0.55-1.0 mm longis, 0.4 mm latis. Flores 6-8 in umbellis lateralibus, sublazulini vel subrosei vel lactei. Bracteae inflorescentiae 2, rotundatae, ciliatae, 1.7-2.0 mm diametro, evanescentes. Pedunculus 1-3 mm longus, pedicellis 2.2-5.0 mm longis. Calyx rotatus, glabrus, 3-5 mm diametro, sepalis ovato-deltoideis, 1.0-1.5 mm longis. Discus glandularis violaceus, 1.5 mm diametro. Stylus 1.5-1.8 mm longus, stigmate trilobato, lobis circa 0.1 mm longis. Filamenta staminum 1.4-1.8 mm longa, antheris 0.8 mm longis. Petala unguiculata, 2 mm longa, leniter deflexa, laminis cyathiformis 1 mm longis. Capsula globosa, circa 3.3 mm diametro, rubella ubi immatura, brunnea hebetata ubi matura, cornibus lateralibus absentibus vel raro vestigialibus, cristis intermediis absentibus. Semina 3, politae, brunneae ad fusco-nigras, 2.2 mm longae. Florescentia in circa medio Februario ad Martio, fructibus maturescentibus post 2.5-3.0 menses.

TYPE: U.S.A. California: Riverside Co., Vail Lake area, 1 mile W of lake, T8S, R1W SE 1/4 Section 8, SW 1/4 SW 1/4 section

9; 2000-2099 feet. Restricted to series of N-facing slopes. 19 March 1989, Steve Boyd, Tim Ross, Laurel Arnseth 3020 (HOLOTYPE: RSA; Isotypes: CAS, MO, SD, SJSU, UC, UCR, US, and 14 others to be distributed).

Paratypes. - U.S.A. California: Riverside Co., same location as above, 12 March 1989 (fl.), Steve Boyd, Tim Ross, Laurel Arnseth 2960 (CAS, MO, SJSU, RSA, UCR); same location as above, 31 March 1989 (fr.), Steve Boyd, Tim Ross, Laurel Arnseth 3097 (CAS, MO, RSA, SD, SJSU, UC, UCR, US, and 14 others to be distributed).

Rounded, divaricately branched shrub, (3.0-) 12-15 (-20.) dm tall. Basal stems one to several, with the main trunk to 7.2 cm in diameter and eventually developing a braided appearance. Bark relatively smooth, ash gray to slate gray or occasionally ranging to reddish brown on exfoliating trunks. Young twigs reddish brown maturing to ashy gray with internodes (2.0-) 2.5-7.0 (-13) mm in length. Stipules on new growth are reddish brown, ultimately becoming iron gray with a corky texture. Leaves glabrous, coriaceous, yellow green to medium green, opposite on stems of recent growth, becoming fascicled on short axillary spur branches in older wood; narrowly oblanceolate to obovate, (2.0-) 3.5-7.0 mm long, (1.0-) 1.5-2.5 (-3.0) mm wide, 0.8-1.0 mm thick; the adaxial surface shallowly concave folded; abaxial surface strongly convex, ± gibbous; the margins entire, or occasionally with 1-2 (-3) pairs of minute teeth; the apex bearing a tooth, or rounded, or emarginate. Midrib visible on abaxial surface, but lateral veins generally obscured. Petioles 0.55-1.0 mm long, 0.4 mm wide, sparsely appressed pubescent in youngest leaves but soon glabrous. Inflorescences axillary on peduncles 1-3 mm long, mostly 6-8 flowered. Floral bud scales 2, pinkish, broadly ovate to orbicular, 1.7-2.0 mm long, sparsely puberulent abaxially towards the apex, with ciliate margins; evanescent. Peduncles 1-3 mm long. Pedicels 2.2-5.0 mm long, usually deeply pigmented at anthesis. Calyx at anthesis 3-5 mm broad, glabrous, the lobes ovate-deltoid, 1.0-1.5 mm long. Flowers pale blue or rarely pinkish lavender, fading to white after anthesis due to loss of pigmentation in pedicel and glandular disk. Petals ladle shaped, 2 mm long, equally divided between the filiform claw and the deeply saccate blade. Style 1.5-1.8 mm long, trilobate, each lobe circa 0.1 mm long. Staminal filaments 1.4-1.8 mm long; anthers 0.8 mm long. Capsule globose, 3.3 mm in diameter, hornless or rarely with 3 rudimentary lateral horns; shiny and ± reddish when young, becoming dull light brown when mature. Seeds medium to dark brown with polished surfaces, convex abaxially, angled on inner face; 2.2 mm long. Flowering occurs in approximately mid-February to March, with maturation of the capsules in about late May to mid-June.

Close observation of the rounded leaf margins reveals a distinctive pattern resembling the labial scales about the mouths of some snake species. This characteristic patterning served as the inspiration for the specific epithet, ophiochilus (Greek, ophis [snake, serpent]; cheilos [lip]). Because the sole population overlooks Vail Lake, we would like to suggest the name "Vail Lake Ceanothus" as the vernacular for this species.

### DISCUSSION

Ceanothus ophiochilus is known only from the type locality where it grows on a series of contiguous north-facing slopes and ridge tops between 1980' and 2090' on the eastern slopes of Oak Mountain', 1 mile west of Vail Lake. The entire population is restricted to about 20 acres of a pyroxenite rich outcrop which totals about 40 acres in area. It is surprising that a plant as distinctive as C. ophiochilus could remain undetected in a region as relatively well explored botanically as Southern California. Historical factors have certainly played a role in this regard. The Vail Lake area has long been inaccessible to botanists, having been a part of the sprawling Vail Ranch and later held in private ownership by recreational vehicle parks and now developers. The area did receive some attention from such notable botanists as Philip Munz, F.W. Peirson, Marcus E. Jones, and Edmund Jaeger during the early part of this century. However, at that time, the C. ophiochilus population, which is surrounded by dense chaparral on all sides, would still have been some distance from any contemporary access roads. It is likely that past botanical exploration in this region has been confined to those areas most readily accessible from the main highways. An extensive area from Mount Palomar northward to Bautista Canyon apparently remains completely unexplored botanically.

It appears unlikely that other populations of Ceanothus ophiochilus exist, however. The Oak Mountain pyroxenite rich outcrop is unusually large, yet it has not been reported by geologists working in the area (Morton 1989, pers. comm.; Seay 1964; Mann 1955; Rogers 1965). Morton (1989, pers. comm.) indicated that other large pyroxenite rich outcrops are not known from the surrounding area and that the presence of similar large outcrops is doubtful. He suggested a possible link between the outcrop and past thermal activity associated with a small, extinct volcano of late Pleistocene or sub-Recent age (Mann 1955) at the mouth of Temecula Creek Canyon, approximately 1 mile to the northwest. No distinction of soil type is indicated by U.S. Soil Conservation Service maps (Knecht 1971). However, Tullock, et. al. (1989, pers. comm.) found that soil samples taken within the areas supporting C. ophiochilus were deficient in phosphorus, with ridgetop soils having no detectable amounts.

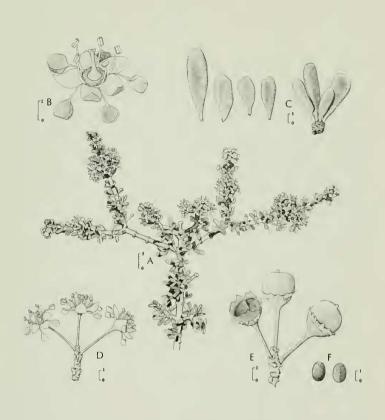
<sup>&#</sup>x27;[Note: The name "Oak Mountain" has been applied by the USGS to two important physical features in the Vail Lake area; in this case we refer to the 2130-foot "Oak Mountain" (USGS 7.5' Vail Lake quadrangle) which corresponds to Mann's (1955) "Vail Mountain" vs. the 2705-foot "Oak Mountain" north of Vail Lake (USGS 7.5' Sage quadrangle).]

Ceanothus ophiochilus is unique among the Cerastes taxa from Southern California in having blue to pinkish lavender flowers rather than the usual white to cream white. However, the leaves are the most striking morphological feature of C. ophiochilus and unequivocally distinguish it from all other taxa in section Cerastes. No other species in the section is reported to have leaves as small and narrow, and no other species in either section of Ceanothus has been reported to possess leaves with a strongly gibbous lower surface (Figure 2, Figure 3). Another morphological feature apparently unique to C. ophiochilus relative to other members of section Cerastes is the general lack of pubescence, especially on the abaxial leaf surface. Except for the very youngest leaves at growth tips, leaf pubescence is limited to the trichomes guarding the entrance to each stomatal crypt (Figure 3, Figure 4). Stomatal crypt structure appears to be Type II as defined by Nobs (1963), with the trichomes confined to the border of the crypt aperture.

The tiny, fascicled leaves of Ceanothus ophiochilus give vegetative plants a strikingly similar appearance to Adenostoma fasciculatum Hook. & Arnott, the codominant shrub at the type locality. This condition may also help to explain the relatively late discovery of this species. Except during the brief flowering period, C. ophiochilus is difficult to differentiate from the surrounding Adenostoma without relatively close examination.

Using McMinn's (1942) treatment of the genus, Ceanothus ophiochilus keys to C. ramulosus (E. Greene) McMinn var. fascicularis McMinn. This is based on the shared characters of hornless capsules, relatively entire leaf margins, leaves borne in axillary fascicles in older wood, and light blue to pale lavender flowers. That taxon, however, is endemic to coastal terraces in Santa Barbara and San Luis Obispo counties, California, and differs in having slender, spreading branches; a larger capsule (4.7 mm); and larger (6-20 mm), planar leaves which are dark green on the upper surface and minutely canescent on the lower surface (McMinn 1942; Munz 1959). Ceanothus ramulosus var. fascicularis also differs in possessing Type I stomatal crypts (Nobs 1963).

Using Munz's (1974) floristic treatment for southern California, Ceanothus ophiochilus keys (albeit not smoothly) to C. greggii A. Gray. This is based primarily on the concave upper leaf surface and relatively small, lateral horns on the capsules (at most, vestigial in C. ophiochilus, but also vestigial in some forms of C. greggii). Ceanothus greggii is a highly variable, primarily desert, species which ranges from Oaxaca, México, in the south, northward through the Chihuahuan, Sonoran, Mojave, and Great Basin Deserts, as well as into the arid interior cismontane regions of southern California (McMinn 1942). The species is represented by three more-or-less geographically defined varieties: the typical var. greggii; var. vestitus (E. Greene) McMinn; and var. perplexans (Trelease) Jeps. (McMinn 1942). Variety greggii ranges northward from Oaxaca, México, into Texas, New Mexico, and Arizona. Variety vestitus ranges northward from Arizona through Nevada and Utah, and westward into Cali-



## CEANOTHUS OPHIOCHILUS (RHAMNACEAE): A DISTINCTIVE, NARROWLY ENDEMIC SPECIES FROM RIVERSIDE COUNTY, CALIFORNIA

Steve Boyd, Timothy Ross. Laurel Arnseth

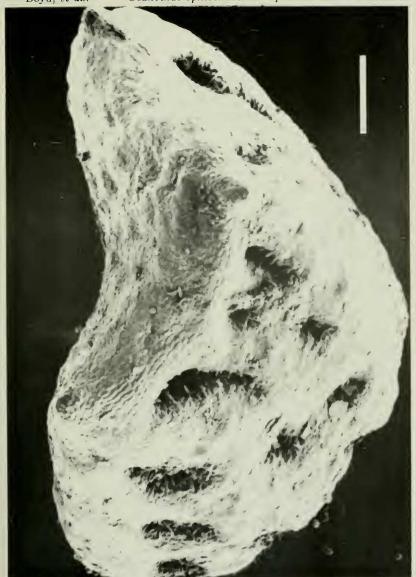
Figure 1. Ceanothus ophiochilus Boyd, Ross, & Arnseth, sp. nov. A) Flowering stem illustrating divaricate branching pattern and fascicled leaves on older wood. B) Flower detail. Glandular disk surrounding ovary provides much of the floral color. C) Leaf fascicle and four leaves removed from one plant to show variation in size. shape, and margin. Note vestigial marginal teeth on several leaves. D) Inflorescence (lower flowers removed). E) Infructescence, one capsule having dehisced. F) Individual seed, abaxial and adaxial views. Scale bar increments = 1mm.



CEANOTHUS OPHIOCHILUS (RHAMNACEAE): A DISTINCTIVE,
NARROWLY ENDEMIC SPECIES FROM RIVERSIDE COUNTY, CALIFORNIA

Steve Boyd, Timothy Ross, Laurel Arnseth

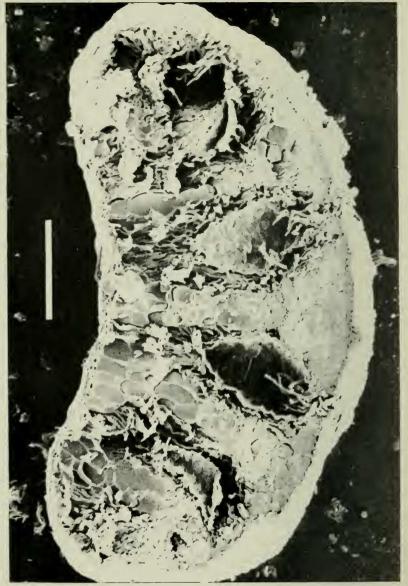
Figure 2. In situ photograph of Ceanothus ophiochilus in late anthesis showing early fruit development. Photo taken April 1, 1989.



### CEANOTHUS OPHIOCHILUS (RHAMNACEAE): A DISTINCTIVE, NARROWLY ENDEMIC SPECIES FROM RIVERSIDE COUNTY, CALIFORNIA

Steve Boyd, Timothy Ross, Laurel Arnseth

Figure 3. SEM photograph showing a near-apical view of *Ceanothus ophiochilus* leaf with three vestigial teeth, one apical and two marginal. Note the glabrous surfaces, pubescence being limited to the entrances of the stomatal crypts. Scale bar = 200 microns.



### CEANOTHUS OPHIOCHILUS (RHAMNACEAE): A DISTINCTIVE. NARROWLY ENDEMIC SPECIES FROM RIVERSIDE COUNTY, CALIFORNIA

Steve Boyd, Timothy Ross, Laurel Arnseth

Figure 4. SEM photograph of cross-section through a Ceanothus ophiochilus leaf illustrating concave upper surface, rounded margins, strongly convex underside, and relatively large, Type II stomatal crypts with trichomes limited to the crypt aperture. Photosynthetic mesophyll is apparently limited to the area immediately surrounding the stomatal crypts with most of the remaining area occupied by bundle sheath extension cells. Scale bar = 200 microns.

fornia through the Mojave Desert ranges as far as southern San Luis Obispo County. Variety perplexans occurs in California from the southern slopes of the San Bernardino and Little San Bernardino Mountains southward through the peninsular ranges into northern Baja California. This third taxon occurs as a common element in desert transition chaparral vegetation on the Anza Bench, less than 10 miles east of Vail Lake.

Ceanothus greggii differs from C. ophiochilus in possessing larger leaves (9-19 mm long, 6-9 mm wide) which are not fascicled in older wood, and which are grayish canescent on both surfaces in vars. greggii and vestitus and on the lower surface in var. perplexans. These taxa also differ from C. ophiochilus in possessing Type III stomatal crypts (Nobs 1963). Likewise, the capsules are generally larger (3-5 mm in diameter), and the flowers are white.

In overall morphological aspect, Ceanothus ophiochilus more closely approaches C. greggii than C. ramulosus var. fascicularis. The shallowly concave folded upper leaf surface of C. ophiochilus suggests a xeromorphic reduction of C. greggii (s.l.) leaves and the yellowish green leaf color is similar to that in C. greggii var. perplexans. Likewise, the branching patterns of C. ophiochilus and C. greggii are similar. On the basis of shared morphological features, it would appear that the closest affinities of C. ophiochilus may lie with the C. greggii complex. We are hesitant, however, to speculate further on the relationships or possible origins of C. ophiochilus solely on the basis of morphology. The complexities inherent in edaphic endemism (Raven 1964; Mason 1946a,b) may, in this instance, be further complicated by hybridization and introgression with contemporary sympatric Ceanothus species over geologic time. The relationships of C. ophiochilus to other taxa in the section would best be elucidated through a comprehensive analysis of introgressive hybridization and reticulate evolution within the section as a whole.

The xeromorphic features exhibited by Ceanothus ophiochilus, especially reduction of leaf size, plant stature, and pubescence, correspond with morphological responses to serpentine substrates as exhibited by numerous other taxa (Kruckeberg 1984). While the Oak Mountain substrate is not serpentine, it is similar to many serpentine outcrops in its rocky, poorly developed soil strata, low levels of calcium, and extremely low amounts of available phosphorus (Kruckeberg 1984). Because of the combination of harsh physical features and the stresses related to the chemical composition of the soil, it is not unexpected to observe similar morphological responses on the Oak Mountain outcrop.

Today, selective survivability on this substrate may play an important role in maintaining the integrity of Ceanothus ophiochilus as a distinct species. Extensive interspecific hybridization is well known in Ceanothus, especially in section Cerastes (McMinn 1944; Nobs 1963). It is not surprising, therefore, that several individuals of suspected hybrid origin were located within the C. ophiochilus population (Boyd, Ross, & Arnseth Nºs 3017, 3018, 3098, 3099 [all

RSA)). Large populations of C. crassifolius Torr. are present on sedimentary substrates less than one-half mile to the south and east of the C. ophiochilus population. In 1989, anthesis in the C. crassifolius populations in the Vail Lake area overlapped and extended beyond that of C. ophiochilus; consequently, it appears that ample opportunity exists for gene flow between the two taxa. Ceanothus crassifolius differs considerably from C. ophiochilus in characters and general appearance. This white flowered species is a stout, erect, openly branched shrub 2.0-3.5 m in height with tomentose twigs. Leaves are broadly elliptic to ± elliptic obovate, 15-30 mm long, strongly revolute to nearly planar, olive green and glabrous above, and white tomentose beneath. The viscid fruits are globose with short (but prominent), subdorsal horns and are 7-8 mm broad (Munz 1959). Ceanothus crassifolius does, however, share with C. ophiochilus the Type II stomatal crypt (Nobs 1963). The hybrid plants that we observed displayed various stages of intermediacy between these two taxa. Interestingly, all suspected hybrids were found growing at the margins of the C. ophiochilus population, near the contact zone with adjacent metasedimentary substrates.

The species of Ceanothus section Cerastes lack the ability to crown-sprout and only reproduce from seeds stored in the soil, generally in response to fire or physical disturbance (Hadley 1961; Raven 1977). We suspect that C. ophiochilus, while occasionally hybridizing with C. crassifolius, is maintained in relatively pure stands due to differential establishment of seedlings following fire. Ceanothus ophiochilus is probably better able to tolerate the unusual edaphic conditions present on the outcrop than is the regionally more abundant C. crassifolius. Apparently, hybrid individuals become established and flourish only at the margins of the outcrop where unfavorable edaphic conditions have been ameliorated.

The long term prospects for the continued existence of Ceanothus ophiochilus in the wild are uncertain at this time due to the threat of human encroachment. Southwestern Riverside County is currently undergoing some of the most rapid urbanization anywhere in the state and, regrettably, C. ophiochilus occupies a locality now considered suitable for development. It does not stand alone. The Vail Lake region also harbors the largest known populations of both the state listed Mahonia nevinii (A. Gray) Fedde [= Berberis nevinii A. Gray] and the federally listed Dodecahema leptoceras (A. Gray) Reveal & Hardham [= Centrostegia leptoceras A. Gray; Chorizanthe leptoceras (A. Gray) S. Watsonl, as well as significant populations of several other sensitive taxa (Boyd, Arnseth, & Ross 1989). While these other taxa occur elsewhere in limited numbers, the development of the site on which the sole population of Ceanothus ophiochilus occurs would result in the extirpation of the species in its wild state. Even partial development of the land surrounding the site presents a serious threat to the species. Changes in fire regime, either through suppression or through the introduction of unnaturally more frequent burns, could prove disastrous. Likewise, given the unique dynamics involved between the

species and its substrate, we completely reject ex-situ preservation alone as an option, especially given the degree to which Ceanothus are known to hybridize in the artificial confines of cultivation. We recommend that any development plans implemented in the region provide reasonable and effective protection for these plants.

Ceanothus ophiochilus should be immediately added to list 1B of the California Native Plant Society's Inventory of Rare and Endangered Vascular Plants with a R-E-D code of 3-3-3, its most sensitive rating. The species is limited to a solitary, highly restricted population; is endemic to the state of California; and is currently endangered by proposed development of the area. In addition, we strongly urge the immediate listing of Ceanothus ophiochilus as an endangered species by the California Department of Fish and Game, and by the United States Fish and Wildlife Service to provide this species the greatest legal protection possible from encroachment by human activities.

#### ACKNOWLEDGMENTS

We express our thanks to Dr. Clifford Schmidt, Dr. Sherwin Carlquist, and Andrew C. Sanders for reviewing this manuscript and offering various comments and suggestions. Special thanks to Kendall for providing the excellent line drawing in spite of our pitiably low budget. Thanks to Dr. Robert Tullock, Leta Barber, Vince Gallegos, and Matt Riha for having devoted so much time to analyzing soil samples from the Vail Lake site. Thanks also to Dr. Douglas Morton for personal observations relative to the geology of western Riverside County with specific regard to the substrate at the site, to Dr. Carlquist for providing the SEM photos, and to Dr. Scott Zona, Michael Hanson, Hugo Cota, and several others for assistance in various ways.

### REFERENCES

Boyd, Steven D., Laurel E. Arnseth, & Timothy S. Ross. 1989. Botanical assessment of Bedford Properties holdings surrounding Vail Lake, Pauba Valley, Western Riverside County, California (Technical Appendix A). 51 pp. In Nelson, S. Gregory, S.D. Boyd, L.E. Arnseth, & T.S. Ross. 1989. Biological assessment of Bedford Properties holdings surrounding Vail Lake, Pauba Valley, Western Riverside County, California. Riverside County Planning Department, Riverside, California. 124 pp.

Hadley, Elmer B. 1961. Influence of temperature and other factors on Ceanothus megacarpus seed germination. Madroño 16:132-138.

- Knecht, Arnold A. 1971. Soil survey of western Riverside area, California. Soil Conservation Service, U. S. Government Printing Office, Washington, D.C. 216 pp.
- Kruckeberg, Arthur R. 1984. California Serpentines: Flora, Vegetation, Geology, Soils, and Management Problems. University of California Press, Berkeley, California. 180 pp.
- Mann, John F., Jr. 1955. Geology of a portion of the Elsinore Fault Zone, California. California Division of Mines and Geology Special Report 43. 22 pp.
- Mason, Herbert L. 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. Madroño 8:209-226.
- \_\_\_\_\_. 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. Madroño 8:241-257.
- McMinn, Howard E. 1942. A systematic survey of the genus *Ceanothus*. pp. 131-304 in Van Rensselaer, Maunsell & H. E. McMinn, 1942. *Ceanothus*. Santa Barbara Botanic Garden, Santa Barbara, California. 308 pp.
- Morton, Douglas M. 1989. Personal Communication. Department of Geology, University of California, Riverside, California.
- Munz, Philip A. 1974. A Flora of Southern California. University of California Press, Berkeley, California. 1086 pp.
- La David D. Keck. 1959. A California Flora. University of California Press, Berkeley, California. 1681 pp.
- Nobs, Malcolm A. 1963. Experimental studies on species relationships in *Ceanothus*. Carnegie Institution of Washington Publication 623. Washington, D.C. 94 pp.
- Raven, Peter H. 1964. Catastrophic selection and edaphic endemism. Evolution 18(2):336-338.
- . 1977. The California flora. 30 pp. in Barbour, Michael G. & Jack Major. 1977. Terrestrial Vegetation of California. John Wiley & Sons, New York. 1002 pp.
- Rogers, Thomas H. 1965. Geologic map of California, Santa Ana sheet. California Division of Mines and Geology. Scale 1:250,000.

- Seay, Mervyn W. 1964. Geology of the Aguanga Basin in the vicinity of Vail Lake, southern Riverside County, California [Bachelor's Thesis]. University of California, Riverside, California. 57 pp.
- Tullock, Robert, Leta Barber, Vince Gallegos, & Matt Riha. 1989. Personal Communication. Department of Soil Science, California State Polytechnic University, Pomona, California.